BREEDING BIOLOGY OF TRISTRAM'S STORM-PETREL ON LAYSAN ISLAND

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ABSTRACT. – Breeding biology of Tristram's Storm-Petrels (*Oceanodroma tristrami*) was studied on Laysan Island in the Northwestern Hawaiian Islands from 3 February to 14 June 1991. Adults arrived on Laysan from mid-October to November. Most egg laying occurred in December and January and hatching in February and March. The young fledged from late April to early June at 85–92 days of age. Their growth rate was best described by the logistic curve. Adults did not begin molt of remiges until after the breeding season. Eggs hatched at only nine of 27 nests (33%) found during incubation; five of these hatchlings fledged (56%). Abandonment rates were identical at nests where we handled adults and where we inspected eggs without handling adults. Because unattended eggs were destroyed quickly by Laysan Finches (*Telespiza cantans*), we suggest that Tristram's Storm-Petrels that co-occur with finches seldom neglect their eggs as is common among other species of storm-petrels. Modifications caused by reaching into a burrow (e.g., widening the entrance and dislodging soil from burrow walls) may be perceived by adult storm-petrels as a signal that the burrow may collapse. *Received 17 Dec. 1991, accepted 1 April 1992.*

Tristram's Storm-Petrel (*Oceanodroma tristrami*) is one of the least known of the northern hemisphere storm-petrels. Its range is restricted to the western and central North Pacific Ocean, with the largest numbers (perhaps 2000–4000 pairs) occurring on Nihoa, Laysan, and Pearl and Hermes Reef in the Northwestern Hawaiian Islands (Rauzon et al. 1985, Harrison 1990). Smaller numbers nest on the Izu and Volcano islands of Japan. The pelagic distribution of Tristram's Storm-Petrel is thought to be confined to waters near and north of the breeding islands and to the expanse of ocean between Hawaii and Japan (Crossin 1974, AOU 1983, Harrison 1987). Because it nests in winter when access to remote islands is difficult, little is known about its breeding biology. Indeed, virtually all published accounts of Tristram's Storm-Petrel in Hawaii are based on brief visits to breeding islands (e.g., Ely and Clapp 1973, Amerson et al. 1974, Crossin 1974, Rauzon et al. 1985) or on inferences drawn from other species of hydrobatids (viz Harrison 1990).

In this paper, we describe aspects of the breeding biology of Tristram's Storm-Petrel on Laysan Island in the Northwestern Hawaiian Islands. We also discuss how an endemic egg predator, the Laysan Finch (*Telespiza cantans*), may influence nesting success and incubation behavior of adults. Lastly, we present a hypothesis as to why incubating storm-petrels are so sensitive to human disturbance.

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STUDY AREA AND METHODS

Laysan Island (25°46'N, 171°44'W) is a low (elevation <12 m) coral island located about 1500 km WNW of Honolulu, Hawaii. The island has an area of 397 ha, including a 70-ha hypersaline lake. Laysan Island is part of the Hawaiian Islands National Wildlife Refuge and is uninhabited except when researchers are present. Approximately 47% of the island is vegetated (Morin and Conant 1990). The most abundant plant is a native bunchgrass (*Eragrostis variabilis*). Ely and Clapp (1973) and Morin and Conant (1990) provide a more detailed description of the island, including a complete list of plants. From late winter to early spring 1991, Laysan was mostly windy (often 20–30 knots) and dry (<6 cm of rain in February and March); temperatures ranged from 14–25°C in February, 16–27°C in March, and 19–30°C in April and May (J. S. Marks, unpubl. data).

Marks noted autumn arrivals of storm-petrels in 1988 and 1990. In 1991, we visited Laysan from 3 February to 14 June; all observations of nesting storm-petrels occurred during this visit. We did not attempt to census the number of breeding storm-petrels on Laysan, and we monitored only a few of the nests there. Nests were located during daytime by searching for burrows on the ground surface and beneath clumps of *Eragrostis*.

Initially, we removed incubating adults from their burrows for about 5–8 min for banding, weighing, and measuring. After several nests failed (presumably from abandonment; see below), we inspected nests by removing eggs without handling the adults. Eggs were returned to incubating adults in 1–2 min. Eggs were checked every 2–5 days until they were starred and then every 1–2 days until hatching. Adults always remained in their burrows during egg checks and immediately settled upon their eggs when we returned the eggs to the burrows.

We also caught adults at night on the ground surface. We measured body mass (± 1 g using a 100- or 300-g Pesola spring balance), wing chord (± 1 mm using a stopped ruler), exposed culmen length (± 0.1 mm), tarsus length (± 0.1 mm), and scored molt of flight feathers for 80 adults caught during February. Adults caught in April and May (N = 50) were weighed and inspected for molt but were not banded or measured.

Beginning the day after hatching, nestlings were weighed (± 1 g) every seven days between 14:00 and 17:00 h HST. We fitted nestling mass data to three sigmoid growth models (logistic, Gompertz, and von Bertalanffy) using nonlinear least squares regression (SYSTAT NONLIN; Wilkinson 1986) and estimated growth parameters (i.e., the growth constant *K*, asymptotic mass, and initial mass) from the model that yielded the lowest residual mean square error (Ricklefs 1983). We also calculated t_{10-90} , which is the amount of time required to grow from 10 to 90% of the asymptotic mass (Ricklefs 1967).

Adult vocalizations were recorded with a Marantz PMD 201 cassette recorder (tape speed 4.75 cm sec⁻¹) and a parabolic microphone. Recordings were made of birds vocalizing from inside burrows or from the ground surface. Sonograms were prepared on a computer using MacRecorder software.

Statistical tests (two-tailed) were based on Zar (1984); data were log-transformed when appropriate. Differences were considered significant as $P \le 0.05$.

RESULTS

Timing of breeding and adult attendance at nest colonies. – Adults arrived at and departed from the island only at night. In 1988 and 1990, adults were first heard on the island on 10 and 15 October, respectively, and were numerous by mid-November. Adults had not arrived when Marks left Laysan on 8 September 1989. Most (if not all) of the eggs had been laid by the time we arrived in early February 1991. Several nestlings

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found between 5 and 10 February were \leq one week old. We documented hatching dates at nine nests. Four chicks hatched between 10 and 14 February, three between 22 and 26 February, and one each on 2 and 15 March. Assuming an incubation period of about 45 days (the actual period is unknown), most of the eggs would have been laid in December and January. Eggs were starred for \geq 3–7 days before hatching. Adults attended hatchlings at the nine nests where eggs hatched but were absent at three nests on the day after hatching. Two of these chicks subsequently fledged. Apparently, adults brood nestlings during daytime for no more than 2–3 days after hatching. We did not check nests at night.

Hundreds of adults attended nesting colonies at night during February and March. Many of these birds were nonbreeders that vocalized singly or in pairs from burrows or the ground surface. Adult numbers declined sharply during late April. On 5 May, we found only 13 adults after searching the densest nesting areas for 5 h. Most of the adults that bred successfully probably deserted their chicks between mid-April and mid-May. Most fledglings left the island between mid-April and late May. The latest known departure of a fledgling was 11 June.

Nest and egg characteristics. —Storm-petrel nesting activity was confined to the band of mixed vegetation (*Eragrostis variabilis, Ipomoea pescaprae*, and *Sicyos* sp.) that extended for about 50–250 m around the perimeter of the lake basin in the center of the island. We found 31 burrows with eggs between 5 February and 10 March. Ten were beneath live clumps of *Eragrostis*, eight beneath residual clumps of *Eragrostis*, six among *Ipomoea* or *Sicyos*, and seven in bare sand near vegetation. Burrows were about 8–10 cm in diameter at the entrance and ranged from 20 cm to at least 80 cm in length (i.e., the maximum length we could reach).

Eggs were white and often had a faint ring of tiny red spots near the blunt end (but see Rauzon et al. 1985). Thirty eggs had a mean length (L) of 3.88 cm \pm 0.16 (SD; range = 3.48–4.28) and a mean breadth (B) of 2.80 cm \pm 0.13 (range = 2.52–3.17). Egg volumes (V = 0.507LB²; Hoyt 1979) ranged from 11.2 to 21.8 cm³. These egg measurements are similar to those of Rauzon et al.'s (1985) nine eggs measured on Laysan in 1981.

Nesting success, effects of researcher disturbance, and egg predation by finches. – Eggs hatched at only nine of the 27 nests (33%) found during incubation (excluding nests in four burrows that we stepped on by accident). One chick died while hatching, two chicks died within 14 days after hatching, and one 72-day-old chick disappeared after losing 21 g in a week. The remaining five chicks fledged, for an overall success rate of only 18%. Of the 22 nests that failed during incubation, 12 failed between our first and second visits and five between our second and third visits. This suggests that most of the nest failures during incubation were due

to abandonment in response to our nest visits. Nest abandonments must have occurred at night, because adults never left their burrows during daytime and always returned to their eggs immediately after we released them back into their burrows. The failure rate during incubation was identical (66.7%) at the 18 nests where we handled an adult and at the nine nests where we inspected eggs without handling an adult. Thus, the rate of abandonment was independent of whether we handled adults at their burrows.

Broken eggshells in or near burrows indicated that Laysan Finches destroyed the eggs in all but two of the failures that occurred during incubation. We saw Laysan Finches investigating Tristram's Storm-Petrel and Bonin Petrel (*Pterodroma hypoleuca*) burrows on numerous occasions in February and March. Laysan Finches are well-known predators of seabird eggs (Fisher 1903, Bailey 1956, Ely and Clapp 1973), and this behavior was more prevalent during winter than at any other time of year (J. S. Marks, pers. obs.). Especially during winter, finches probably know the status of most (if not all) of the petrel burrows within their home ranges. Unattended Tristram's Storm-Petrel eggs (at least in burrows <80 cm in length) are probably detected and consumed by Laysan Finches within a day or two of becoming available.

Adult morphology and flight feather molt. - The mean body mass of adults was 92.0 g in February (SD = 8.2, range = 71-112, N = 80), 85.5 g in early April (SD = 5.8, range = 77-97, N = 30), and 83.4 g in early May (SD = 11.2, range = 70–104, N = 20). Body mass differed significantly among months (ANOVA, F = 12.64, df = 2,127; P < 0.0005; data logtransformed). Storm-petrels were heavier in February than in April or May (Tukey test, P < 0.05). Rauzon et al. (1985) also noted a decline in body mass of adult Tristram's Storm-Petrels from winter to spring. Means for the other measurements of the 80 adults caught in February were: wing chord, 179.9 mm (SD = 3.9, range = 172-192); exposed culmen, 18.2 mm (SD = 0.6, range = 16.8-19.5); and tarsus length, 28.4 mm (SD = 0.9, range = 26.4-30.6). Our measurements were similar to those of Rauzon et al. (1985) except for tarsus length, which averaged 2 mm longer (t = 7.22, df = 101, P < 0.0005). This difference was due to Rauzon et al. (1985) measuring to the distal end of the tibiotarsus rather than to the proximal end of the tarsometatarsus (M. J. Rauzon, pers. comm.).

Adults had fresh-looking primaries in February, and we found no indication that they began molting remiges during the breeding season (N = 130 adults inspected between February and early May). Four adults (all apparent nonbreeders) were molting from 1–3 retrices on one side of the tail between 14 and 25 February. Thus, most adults begin molting their flight feathers at sea after the breeding season. We did not check for molt during autumn when the adults first arrived on Laysan. *Encounters with banded adults.* — We caught two storm-petrels that had been banded previously on Laysan. The first, caught on 22 February 1991, was at least three years old when banded on 16 November 1980. The numbers on its aluminum band required chemical etching to be legible. At a minimum age of 14 years, this bird is the oldest known Tristram's Storm-Petrel (previous record was 9 years; Clapp et al. 1982). The second, caught on 28 February 1991, had been banded after its second year on 10 April 1987. Its incoloy band was unworn. Including the two birds noted above, 27 Tristram's Storm-Petrels banded as adults have been recovered in Hawaii, each on the same island at which it was banded (Bird Banding Laboratory, unpubl. data). None of the Tristram's Storm-Petrels banded as nestlings has been recovered.

Nestling development and growth. - Like all hydrobatids, Tristram's Storm-Petrels hatched covered with down and with their eyes closed. The absence of adults at nests soon after hatching suggests that nestlings could thermoregulate at 2-3 days old. The egg tooth disappeared and the eyes opened between days 8 and 15. Mass increased rapidly for five weeks until nestlings reached 121-155% of the average adult mass for February (Fig. 1). Mass remained relatively constant from weeks five to 11 and then dropped to adult mass in the two weeks before fledging (Fig. 1). The five nestlings that we followed from hatching to fledging left the nest at a mean age of 89.2 days (SD = 3.1, range = 85-92) and a mean mass of 93.6 g (SD = 4.0, range = 88-99). Only one nestling gained mass after day 78, suggesting that adults seldom fed their young during the two weeks before fledging. The remiges erupted between days 30 and 35, and the primaries were still in sheath in four of five fledglings. The exception had fully grown primaries on day 90. Fledglings had trace amounts of down or no down adhering to their contour feathers.

Nestling masses obtained after day 78 (when mass began to decline) were excluded from the growth curve analyses. All three growth models provided reasonable parameter estimates (Table 1). The logistic curve yielded the lowest residual mean square error, followed by the Gompertz and the von Bertalanffy curves. The parameter estimates were nearly identical whether derived from the average masses of the five nestlings that fledged or from the average masses of all nestlings of known age (including three that did not fledge). Data presented in Table 1 were derived from the larger sample of nestlings. Growth of individual nestlings that survived to fledging was best described by the logistic curve in three cases and by the von Bertalanffy curve in two cases. On average, nestlings required about 44 days to grow from 10 to 90% of the asymptotic mass (Table 1).

Adult vocalizations. – Tristram's Storm-Petrels produced two main vocalizations, the flight call and the burrow call (Fig. 2). Flight calls were

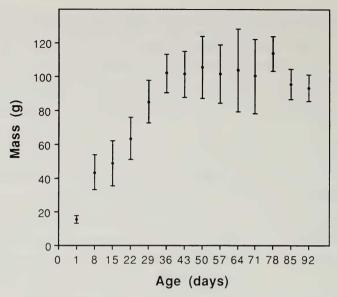


FIG. 1. Average body mass (\pm SD) of Tristram's Storm-Petrel nestlings on Laysan Island, February to June 1991. Samples sizes are 8 (day 1), 7 (day 8), 6 (days 15–71), 5 (days 78–85), and 2 (day 92).

given in flight, on the ground, and in burrows. They consisted of 6-7 syllables of fundamental frequency bands and their overtones (Fig. 2). Burrow calls were given from inside burrows or on the ground but not in flight. They consisted of series of repeated notes that often lasted for > one min. They are similar to the burrow calls of Swinhoe's Storm-Petrel (*Oceanodroma monorhis*) depicted by Taoka et al. (1989b).

Recent studies have revealed sexual dimorphism in the vocalizations of five species of storm-petrels (Simons 1981; James 1984; James and

TABLE 1	
Parameter Estimates (\pm SE) of Three Sigmoid Curves Describing Tristram's Storm-Petrel Nestlings on Laysan Island	
Asymptotic	t ₁₀₋₉₀

Growth model ^b	Growth rate	Asymptotic mass (g)	Initial mass (g)	(days)
Logistic	0.100 ± 0.012	107.1 ± 2.9	18.4 ± 2.3	43.9
Gompertz	0.070 ± 0.011	109.2 ± 4.7	15.1 ± 4.7	44.1
von Bertalanffy	0.060 ± 0.008	110.3 ± 3.8	$20.0~\pm~1.8$	45.7

^a Analyses based on data in Fig. 1 to 78 days of age.

^b The logistic model yielded the lowest residual mean square error; $r^2 = 0.97$.

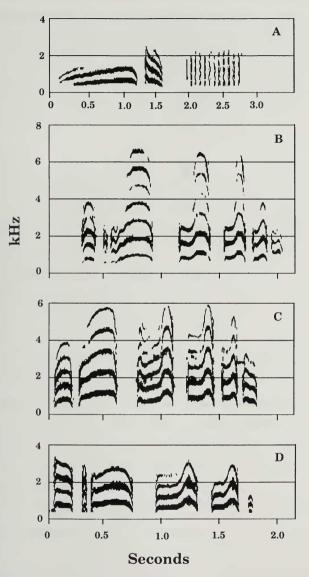


FIG. 2. Sonograms of four adult Tristram's Storm-Petrels on Laysan Island, February 1991: burrow call (A), and flight calls (B–D). The sex of the birds was not known.

Robertson 1985a; Taoka et al. 1989a, b). We could not sex birds by cloacal inspection because we arrived after egg laying, and we did not perform laparotomies. Moreover, we recorded the vocalizations of only a small number of individuals. Thus, we did not determine whether the sex of Tristram's Storm-Petrels can be distinguished by voice. Because procellariiforms that call in flight tend to have sex-specific calls (James and Robertson 1985b), Tristram's Storm-Petrels are good candidates for further research into this phenomenon.

DISCUSSION

Tristram's Storm-Petrels are similar to most other hydrobatids in that they are strictly nocturnal on land, they nest in burrows on remote islands, and they abandon their egg readily when disturbed by humans. Timing of molt is similar to that of other tropical species (Band-rumped Storm-Petrel [Oceanodroma castro] and Wedge-rumped Storm-Petrel [O. tethys]) that do not overlap flight feather molt with the breeding period (Harris 1969, Ainley et al. 1976). Being among the largest of the storm-petrels (Harrison 1987), they lay a larger egg and have a longer nestling period than other species for which data are readily available (Table 2). Harrison's (1990:141) statement that the young fledge in 58-72 days was based on speculation and is incorrect. Rauzon et al.'s (1985) report of "fully-feathered chicks" on Nihoa Island in February suggests that egg laying would have occurred in the first half of October-an extremely early date for this species. Visits to breeding islands from October through January are needed to understand fully the timing of laying and to determine the length of the incubation period in Tristram's Storm-Petrel.

Nest abandonment, egg neglect, and the potential effect of egg predators on storm-petrel incubation behavior. —Storm-petrels often abandon their eggs following disturbance by researchers (e.g., Davis 1957a, Allan 1962, Ainley et al. 1974, Morse and Buchheister 1979, Boersma et al. 1980). Although abandonment is usually permanent, Boersma et al. (1980) observed adult Fork-tailed Storm-Petrels (Oceanodroma furcata) return to eggs 18 and 23 days after abandonment. The poor hatching success (33%) of Tristram's Storm-Petrels on Laysan probably resulted from Laysan Finch predation on abandoned eggs. It is also possible that eggs were destroyed by conspecifics as suggested for Band-rumped and Wedgerumped storm-petrels (Allan 1962, Harris 1969). However, we never found storm-petrels occupying burrows after nest failures, and suitable nesting sites were not in short supply. Moreover, we routinely saw finches going in and out of nesting burrows; presumably, they were searching for unattended eggs to eat.

Storm-petrels (and many other procellariiforms) are also well-known

TABLE 2

Adult Nestling Species mass (g) Egg size (mm) period (days) Source^a Wilson's Storm-Petrel 37.6 33.4×24.2 60 1.2 (Oceanites oceanicus) Black-bellied Storm-Petrel 37.0×27.0 68 3 (Fregetta tropica) 57.5 British Storm-Petrel (Hydrobates pelagicus) 28.0 28.0×21.0 56-73 4.5 Fork-tailed Storm-Petrel (Oceanodroma furcata) 59.2 34.6×26.3 51-66 6,7 Leach's Storm-Petrel 33.0×24.0 59-70 5.8.9 (O. leucorhoa) 41.9 Ashy Storm-Petrel (O. homochroa) 39.6 28.7×21.8 76 8,10 Band-rumped Storm-Petrel 64-78 43.5 31.3×23.1 11, 12 (O. castro) Wedge-rumped Storm-Petrel 27.8×20.6 9 12 (O. tethys) 25.8 Tristram's Storm-Petrel (O. tristrami) 92.0 38.8×28.0 85-92 13

Comparative Data on Adult Mass, Egg Size, and Length of Nestling Period in Storm-Petrels

^a 1 = Beck and Brown (1972); 2 = Roberts (1940); 3 = Beck and Brown (1971); 4 = Davis (1957b); 5 = Cramp (1977);
6 = Boersma et al. (1980); 7 = Simons (1981); 8 = Ainley et al. (1974); 9 = Vermeer et al. (1988); 10 = Dawson (1923);
11 = Allan (1962); 12 = Harris (1969); 13 = this study.

for neglecting their eggs (Richdale 1965, Wilbur 1969, Pefaur 1974, Boersma and Wheelwright 1979). Egg neglect, as distinguished from abandonment, is an adaptive response to the temporary failure of a foraging bird to relieve its mate at the nest. Storm-petrel embryos tolerate chilling, and eggs may hatch after at least seven days of continuous neglect (e.g., Forktailed Storm-Petrel; Boersma and Wheelwright 1979). Five other species of storm-petrels are known to neglect their eggs for 1–5 days (reviewed by Pefaur [1974] and Boersma and Wheelwright [1979]). This behavior is probably widespread among hydrobatids.

Distinguishing abandonment from egg neglect can be difficult. Because most of the failures during incubation occurred soon after we visited a nest, we have assumed that the adults abandoned their nests. If we are correct, then Tristram's Storm-Petrels are highly sensitive to human disturbance. Nests in which we inspected eggs without handling adults had the same high failure rate as nests in which we banded and measured adults. Alternatively, some of the failures we observed may have begun as egg neglect rather than abandonment. Regardless of whether eggs were neglected or abandoned, however, the important point is that unattended storm-petrel eggs on Laysan probably had little chance of hatching owing to predation by finches.

In this regard, a behavior that normally is adaptive in storm-petrels (viz egg neglect) would be selected against wherever storm-petrels and egg predators co-occur. Thus, we predict that Tristram's Storm-Petrels seldom neglect their eggs on Laysan and Nihoa islands, both of which have large numbers of endemic egg-eating finches (the Nihoa Finch [*Telespiza ultima*] is an egg predator; J. S. Marks, pers. obs.). In 1967, Laysan Finches were introduced intentionally on Pearl and Hermes Reef (Conant 1988), which is the only other location in Hawaii with large numbers of Tristram's Storm-Petrels. Thus, a management effort on behalf of finches may have unwittingly reduced the nesting success of storm-petrels (see Conant 1988).

Future studies of Tristram's Storm-Petrel in Hawaii should determine the influence of finches on the nesting success and incubation constancy of storm-petrels and develop means of monitoring storm-petrel nests without causing high rates of abandonment. Such studies should include storm-petrel nesting islands that do not have finches (e.g., Necker Island and French Frigate Shoals).

Why are storm-petrels so sensitive to human disturbance?—We found no explanation in the literature for why human disturbance causes stormpetrels to abandon their eggs so readily. One reason might be that stormpetrels perceive humans to be predators and abandon their nests to avoid predation (P. D. Boersma, pers. comm.). Although this explanation is reasonable for areas where storm-petrels historically co-occurred with predators (including humans), it might not apply to areas like the Northwestern Hawaiian Islands where storm-petrels nest in the absence of predators, thus having no reason to perceive humans as predators. Moreover, if Tristram's Storm-Petrels abandoned nests to avoid "predation" by us, then they should have left their nests soon after we released the birds into their burrows. Instead, they returned to their eggs, and they must not have abandoned their nests until many hours after the disturbance.

We suggest that in some cases, the tendency to abandon a nest is related to nesting in burrows. At least in the sandy substrates common to the Northwestern Hawaiian Islands, burrows collapse occasionally (see also Stokes and Boersma 1991). We have found Bonin Petrels and Wedgetailed Shearwaters (*Puffinus pacificus*) trapped in burrow cave-ins during each of five trips to Laysan since 1988. We suspect that Tristram's Storm-Petrels are similarly vulnerable. Perhaps storm-petrels perceive disturbance as a indication that the burrow is unsound and thus prone to collapse. Storm-petrel burrow entrances are small, and it is difficult to reach into a burrow without altering it (e.g., widening the entrance and dislodging small amounts of soil from the ceiling and sides). Once they discover the disturbance, storm-petrels may respond by abandoning the burrow. Because storm-petrels are long-lived (\geq 31 years for Leach's Storm-Petrel [O. leucorhoa], Klimkiewicz and Futcher 1989), they might be expected to abandon reproductive attempts when faced with the risk of reduced life expectancy (Williams 1966, Goodman 1974). For stormpetrels that nest in sandy substrates, the collapse of a burrow may be just such a risk. For this hypothesis to be valid, abandonment should be uncommon in substrates that are unlikely to collapse. Data from the Galapagos Islands support this view; nest abandonment by Band-rumped and Wedge-rumped storm-petrels following human disturbance is rare (Harris 1969), and the birds nest in holes in lava rock that would be unlikely to collapse. Additional studies are needed to evaluate more fully the relationship between abandonment and nesting substrate in stormpetrels and other burrow-nesting procellariiforms.

ACKNOWLEDGMENTS

We are grateful to K. McDermond (U.S. Fish and Wildlife Service) for permitting us to work on Laysan Island, M. Rauzon for providing data from his study, D. Boersma for information on storm-petrel breeding biology, and R. Redmond and L. Honigman for support and encouragement. E. Greene and D. Lane gave advice on sonogram preparation and growth curve analysis, respectively. Our research has been supported by the U.S. Fish and Wildlife Service (Alaska Fish and Wildlife Research Center, Hawaiian Islands National Wildlife Refuge, Montana Cooperative Wildlife Research Unit), the National Geographic Society, the World Wildlife Fund, the Hawaii Audubon Society, Sigma Xi, a Paul A. Stewart award, and a Curby-Pavelsky-Harris award. Travel to and from Laysan was made possible by the National Marine Fisheries Service, the U.S. Coast Guard, and the NOAA research ship 'Townsend Cromwell.'

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NOTICE TO INDIVIDUALS CONDUCTING RESEARCH IN THE NORTH PACIFIC

Because of a drastic population decline, the Steller sea lion has been listed as a threatened species under the Endangered Species Act. To reduce human disturbance, the National Marine Fisheries Service (NMFS) has placed restrictions on land and water approach in the vicinity of Steller sea lion rookeries in the Bering Sea, Aleutian Islands, and Gulf of Alaska. These prohibitions apply to all individuals and activities unless specifically exempted by NMFS. For further information regarding Steller sea lion regulations, contact NMFS, Protected Resources Management Division, P.O. Box 21668, Juneau, Alaska 99802 (907) 586-7235.